

01 Jan 1998

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Recommended Citation

S. P. Roberts and J. F. Harrison, "Mechanisms of Thermorégulation in Flying Bees'," *American Zoologist*, vol. 38, no. 3, pp. 492 - 502, Oxford Academy, Jan 1998.

The definitive version is available at <https://doi.org/10.1093/icb/38.3.492>

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Mechanisms of Thermoregulation in Flying Bees¹

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SYNOPSIS. Thermoregulation of elevated thorax temperatures is necessary for bees to achieve the high rates of power production required for flight, and is a key factor allowing them to occupy widely varying thermal environments. However, the mechanisms by which bees thermoregulate during flight are poorly understood. Thermoregulation is accomplished by balancing heat gain and heat loss via the following routes: convection, evaporation, and metabolic heat production. There appears to be a diversity of thermoregulatory mechanisms employed during flight among bee species. Some species, particularly *Bombus* spp., actively increase the distribution of thoracic heat to the abdomen during flight as air temperature (T_a) rises, and apparently thermoregulate by varying convective heat loss. However, thermal variation in convection has not been directly measured for any free-flying bee. Above 33°C, flying *Apis mellifera* greatly increase evaporative heat loss with T_a , and many other species “tongue-lash” during flight at high T_a s or when artificially heated. Thus, evaporation seems to be important for preventing overheating during flight at very high T_a s. Flying *A. mellifera* and *Centris pallida* strongly decrease metabolic rate as T_a increases, suggesting that they are varying metabolic heat production for thermoregulation and not aerodynamic requirements. Variation in metabolic heat production appears to be mediated by changes in wingbeat kinematics, since wingbeat frequency decreases with T_a for *A. mellifera* and *Centris* spp. It is unknown if the decrease in flight metabolic rate at higher T_a s occurs secondarily as a consequence of greater efficiency or if it is truly an active response.

INTRODUCTION

Bees (suborder Apoidea) occupy terrestrial habitats representing a wide range of thermal regimes, from tundra above the Arctic Circle to hot deserts and tropical rainforests. An important adaptation that allows them to successfully inhabit these environments is the ability of individuals to regulate elevated, relatively stable thorax temperatures (T_{th}). Thermoregulation is especially important for the purposes of flight, since maximal flight muscle performance occurs within a narrow range of muscle temperatures (Esch, 1976; Coelho, 1991; Gilmour and Ellington, 1993). Despite our knowledge of endothermy in bees and the thermal physiology of bee flight muscle, our understanding of the mechanisms by

which bees thermoregulate during flight remains limited.

Bees exhibit considerable variation in their thermoregulatory ability during flight. The slope of T_{th} on air temperature (T_a) is an indicator of thermoregulatory ability, with a slope of zero indicating perfect thoracic thermoregulation and a slope of one indicating conformance with T_a . In the large (>50 mg) bees studied to date, the slopes of T_{th} on T_a typically range from 0.2 to 0.6 (Table 1). Among bees, the best thermoregulators studied to date are *Centris pallida* males, with a slope of T_{th} on T_a during flight of 0.15 (Roberts, 1996; Roberts, unpublished data), while the tropical bees *Creightonella frontalis* (Stone and Willmer, 1989) and *Euglossa* spp. (May and Casey, 1983), with slopes much closer to one than to zero, may not actively thermoregulate. Larger bees maintain higher T_{th} s than smaller bees during flight at 22°C (Stone and Willmer, 1989), but, surprisingly, body mass explains a small and nonsignificant amount of variation in the slope of T_{th} on T_a for data shown in Table 1 ($r^2 = 0.162$, $P = 0.063$).

¹ From the Symposium *Responses of Terrestrial Arthropods to Variation in the Thermal and Hydric Environment: Molecular, Organismal, and Evolutionary Approaches* presented at the Annual Meeting of the Society for Integrative and Comparative Biology, 26-30 December 1996, at Albuquerque, New Mexico.

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TABLE 1. Regression equations relating thorax temperature vs. air temperature for un tethered flying bees.

Species	Slope	Intercept	Mean body mass (mg)	T _r (°C)	Location/condition	Reference
ANTHOPHORIDAE						
<i>Amegilla sapiens</i>	0.55	21.8	117	16-32	Field	Stone and Willmer, 1989
<i>Anthophora plumipes</i>	0.62	22.4	185	5-26	Feeding and nesting sites	Stone, 1993
<i>Centris pallida</i>	0.32	34.0	165	24-41	Field	Chappell, 1984
<i>C. pallida</i> males	0.15	41.3	122	20-35	Territorial hovering in field	Roberts, unpublished
<i>Xylocopa pubescens</i>	0.21	34.5	642	16-28	Returning to nest	Willmer, 1988
<i>X. sulcatipes</i>	0.32	29.7	422	20-32	Returning to nest	Willmer, 1988
<i>X. varipuncta</i>	0.36	31.7	673	12-41	Temp. controlled room	Heinrich and Buchmann, 1986
<i>X. virginica</i> females	0.23	36.9	510	15-36	Field	Baird, 1986
<i>X. virginica</i> males	0.25	36.8	370	17-36	Field	Baird, 1986
APIDAE						
<i>Apis cerana</i> workers	0.44	28.7	55	12-19	Arriving at feeder, sunny sky	Underwood, 1991
<i>A. cerana</i> workers	0.58	24.7	55	12-20	Arriving at feeder, overcast	Underwood, 1991
<i>A. dorsata</i> workers	0.36	27.7	113	17-25	Arriving at feeder, sunny sky	Underwood, 1991
<i>A. laboriosa</i> workers	0.55	26.5	165	12-20	Arriving at feeder, overcast	Underwood, 1991
<i>A. mellifera</i> workers	0.40	29.6	85	20-40	300 ml chamber	Harrison <i>et al.</i> , 1996
<i>A. mellifera</i> workers	0.44	25.7	84	22-40	Returning to hive	Coelho, 1991
<i>A. mellifera</i> drones	0.45	27.8	200	21-39	Returning to hive	Coelho, 1991
<i>Bombus vosnesenskii</i> queens	0.27	34.7	645	2-35	Temp. controlled room	Heinrich, 1975
<i>Bombus</i> spp.	0.24	29.2	175	20-32	819 ml chamber	Joos <i>et al.</i> , 1991
<i>Bombus</i> spp.	0.56	21.7	149	10-30	Foraging	Joos <i>et al.</i> , 1991
<i>Euglossa</i> spp. males	0.76	17	128	16-30	At scented baits or in jar	May and Casey, 1983
<i>Eufriesea</i> spp. males	0.47	25.8	557	19-29	At scented baits	May and Casey, 1983
MEGACHILIDAE						
<i>Creightonella frontalis</i> females	0.68	18.5	305	20-35	Field	Stone and Willmer, 1989

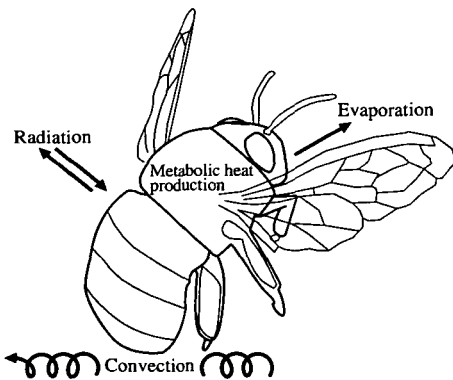


FIG. 1. Routes of heat exchange for an endothermic flying bee.

Apparently, ecological or phylogenetic effects are more important than body size in determining the degree to which bees maintain stable T_{th} during flight.

ROUTES OF HEAT EXCHANGE IN FLYING BEES

Thermoregulation is accomplished by balancing heat gain and heat loss. The various routes of heat flux for a flying bee are illustrated in Figure 1. In cool shady conditions, flying endothermic bees experience a net radiative heat loss, while in warm sunny conditions they experience a net radiative heat gain (Chappell, 1982; Cooper *et al.*, 1985). Potentially, radiative heat transfer may be behaviorally regulated via microhabitat selection. However, to our knowledge, no studies have experimentally addressed this possibility for flying bees. The remainder of this discussion will address variation in the following routes of heat exchange as potential mechanisms of thermoregulation during flight: convection, evaporation and metabolic heat production. These routes of heat exchange have been addressed for flying bees in recent reviews by Heinrich (1993) and Heinrich and Esch (1994). However, our studies of thermal variation in body temperature, water loss, energetics and kinematics in flying bees (Harrison *et al.*, 1996; Roberts, 1996; Roberts, unpublished data) necessitate a re-evaluation of this topic.

Convection

If T_a s are cooler than body temperatures, heat will be lost by convection from the body's surface. Convective heat loss may be varied by changing the air speed over the bee, or by altering the distribution of heat within the bee. During flight, the majority of metabolic heat is produced in the thorax, which represents 30–50% of the bee's body mass and surface area. If all of the metabolic heat is retained within the thorax, there is relatively little surface area for convective heat loss. In contrast, if the heat produced in the thorax is allowed to spread to the abdomen and head, a much greater surface is available for convective heat loss.

An active increase in heat transfer from the thorax to the abdomen can be demonstrated by an increase in the abdominal temperature (T_{ab}) excess ratio, $(T_{ab} - T_a) \div (T_{th} - T_a)$, termed R_{ab} , at higher T_a s (Baird, 1986; Fig. 2A). In other words, if more heat is transferred from the thorax to the abdomen at higher T_a s, then T_{ab} and T_{th} will tend to converge as T_a s increase. Use of active variation in heat transfer between the thorax and abdomen as a thermoregulatory mechanism appears to be highly variable in bees and, based on the data available, not explained by phylogeny (Fig 2B). A positive relationship between R_{ab} and T_a has been observed during flight in *Bombus terreicola* (Heinrich, 1972a), *B. vagans* (Heinrich, 1972b), *B. vosnesenskii* (Heinrich, 1975), pooled *Eulaema* and *Eufriesea* spp. (May and Casey, 1983) and the solitary bee *Anthophora plumipes* (Stone, 1993; Fig 2B). For *B. terreicola* and *B. vagans*, R_{ab} is higher for bees flying in sunny conditions than for bees flying in shady conditions (Heinrich, 1972a), indicating a thermoregulatory response to radiant heat load. However, for *B. vagans*, R_{ab} increases with T_a only for bees flying in sunny conditions. In *A. plumipes*, the abdominal temperature excess ratio becomes independent of T_a s above 18°C, suggesting that the ability of *A. plumipes* to transfer heat to the abdomen reaches its maximum at this T_a . Thermoregulation by varying heat transfer between the thorax and abdomen has also been reported for *Xy-*

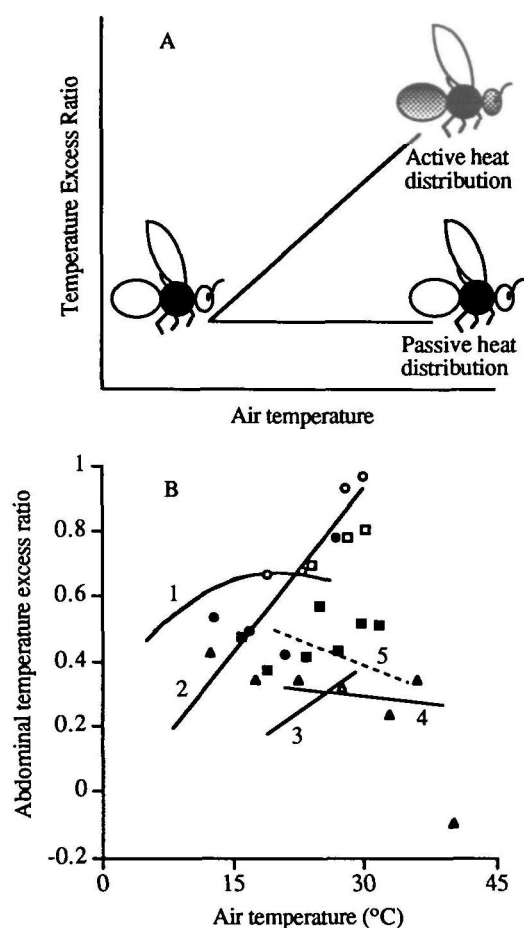


FIG. 2A. If heat is actively distributed from the thorax to the head or abdomen at high T_a s, then $(T_x - T_a) \div (T_{th} - T_a)$ increases with T_a , where T_x is the temperature of the head or abdomen (Baird, 1986). If heat is passively distributed from the thorax to the head or abdomen across T_a , then $(T_x - T_a) \div (T_{th} - T_a)$ remains constant across T_a . Figure 2B. Abdominal temperature excess ratios (R_{ab}), defined as $(T_{ab} - T_a) \div (T_{th} - T_a)$, plotted as a function of T_a for flying bees. Line 1 is calculated from regressions of T_{th} and T_{ab} on T_a for *Anthophora plumipes* (Stone, 1993). Line 2 is calculated from regressions of T_{th} and T_{ab} on T_a for *Bombus vosnesenskii* (Heinrich, 1975). Line 3 is calculated from regressions of T_{th} and T_{ab} on T_a for pooled *Eulaema* and *Eufriesea* spp. males (May and Casey, 1983). Line 4 is calculated from regressions of T_{th} and T_{ab} on T_a for *Apis mellifera* drones (Coelho, 1991). Line 5 is the least square linear regression of R_{ab} vs. T_a (not significant, $r^2 = 0.113$, $P = 0.069$) for *Centris pallida* males (Roberts, unpublished data). The circles represent R_{ab} s calculated from T_{th} s and T_{ab} s of *B. terricola* (Heinrich, 1972a) foraging in the shade (closed circles) and in sun (open circles). The squares represent R_{ab} s calculated from T_{th} s and T_{ab} s of *B. vagans* (Heinrich, 1972b) foraging in the shade (closed squares) and in sun (open squares). The triangles represent R_{ab} s calculated from T_{th} s and T_{ab} s of *A. mellifera* workers (Cooper *et al.*, 1985).

locopa californica (Chappell, 1982), but does not appear to occur in *Apis mellifera* (Heinrich, 1980a, b; Cooper *et al.*, 1985; Coelho, 1991; Harrison *et al.*, 1996) or *C. pallida* (Fig 2B; Chappell, 1984).

An important assumption of Baird's (1986) model is that heat transfer between each body segment and the environment is driven only by the temperature differential between the body segment and environment (see also Stavenga *et al.*, 1993). If evaporative water loss greatly increases at high T_a s so that its effect on T_{ab} is greater than its effect on T_{th} , then R_{ab} will be a poor indicator of active heat distribution from the thorax to the abdomen. For example, *A. mellifera* workers experience large increases in evaporative heat loss at high T_a s (see below), which is likely responsible for the dramatic drop in its R_{ab} as T_a rises from 35 to 40°C (Fig. 2B; Cooper *et al.*, 1985). Thus, caution is urged when using R_{ab} as an indicator of active heat distribution.

The mechanism by which heat transfer between the thorax and abdomen is actively varied has been described only for one species. In *B. vosnesenskii*, the regulation of heat transfer from the thorax to the abdomen is accomplished by circulatory variations of hemolymph flow in the petiole, the narrow region between the abdomen and thorax (Heinrich, 1976). At low T_a s, hemolymph flow from the thorax to the abdomen (below the ventral diaphragm) and from the abdomen to the thorax (within the heart) occurs simultaneously, and the resulting counter-current exchange of heat in the petiole retains most of the heat in the thorax. At high T_a s, forward and reverse flows alternate, greatly reducing the amount of counter-current heat exchange in the petiole and allowing hemolymph to transfer large amounts of heat from the thorax to the abdomen.

Higher airspeeds over the body will enhance convective heat loss by reducing the thickness of the boundary layer. In theory, a flying bee could thermoregulate by varying wing kinematics or flying faster at high T_a s. In a temperature-controlled room, the carpenter bee *X. varipuncta* flies faster at higher T_a s, suggesting that it may increase convective cooling by this mechanism

(Heinrich and Buchmann, 1986); however, the authors made no empirical measures of flight speeds. The large, flat head of *Xylocopa* spp. forms a broad surface contact area with the thorax, and the sensitivity of *X. varipuncta* head cooling constants to airspeeds is 2–3 times greater than for isolated thoraces and abdomens (Heinrich and Buchmann, 1986). Thus, a *Xylocopa* head might act as a heat sink, facilitating high rates of heat loss from the thorax at high airspeeds (Heinrich, 1993; Heinrich and Esch, 1994). Increasing flight speeds at high T_a s may explain the significant negative relationship between head temperature excess ratio and T_a observed in *X. virginica* males (Baird, 1986) and *X. varipuncta* (Heinrich and Buchmann, 1986), although an alternative explanation may be that they are thermoregulating the head (at the expense of T_h regulation) by increasing heat distribution from the thorax to the head at low T_a s (Baird, 1986).

In conclusion, the use of varying heat transfer from the thorax to the abdomen (with subsequent convective heat loss) for thermoregulation during flight is highly variable among bees. There is no convincing evidence for thermoregulatory modulation of convection via changes in airspeed for any bee, though correlative evidence for this mechanism has been shown for carpenter bees. It is important to note that no studies to date have quantified convective heat transfer for a living, flying bee. Several papers have estimated convection from the cooling rates of freshly-killed bees held in a wind tunnel (Chappell, 1984; Cooper *et al.*, 1985; Heinrich and Buchmann, 1986). However, the applicability of these convection values to living, flying bees is unclear, since the wind tunnel method does not account for 1) evaporative cooling from the surface of the dead bee, 2) the complex convective movements associated with the movement of the wings or 3) variation in convection facilitated by circulatory heat exchange between the thorax to the abdomen. Quantifying convection for a living, flying bee should be possible using a heat budget analysis, where the convective heat exchange of a thermally equilibrated bee flying at a given T_a could be calculated by

taking the difference between the measured rates of heat gain (metabolic heat production and radiation) and the measured rates of heat loss (evaporation and radiation). In only one study has metabolism, evaporation and T_h been measured as a function of T_a for a flying bee (Nicolson and Louw, 1982), although a calculation of convection was not performed in this study.

Evaporation

Due to the high latent heat of water, increasing evaporative water loss at higher T_a s has the potential to be a very important component of thermoregulation in flying bees. Increases in evaporative heat loss at higher T_a s can be passive, due to thermal effects on cuticle permeability and the vapor pressure deficit (Hadley, 1994) as well as on body temperature and the vapor density of expiratory air. Active “sweating” across the cuticle has been demonstrated in feeding cicadas (Toolson and Hadley, 1987; Hadley *et al.*, 1989), but no studies have yet tested for such a mechanism in any flying insect. Considerable evaporative water is lost via expired air (Nicolson and Louw, 1982; Louw and Hadley, 1985), and increasing ventilation at higher T_a s could enhance evaporative cooling in a flying bee. Finally, evaporative water loss can also occur via the mouth or anus, although no studies have measured water loss through these routes for flying bees.

The ability to enhance evaporative water loss by regurgitating crop contents onto the labrum or head surface may be widespread in bees. *Xylocopa varipuncta* flying at T_a s near 40°C consistently extend their tongues and “tongue-lash” (Heinrich and Buchmann, 1986), a behavior associated with increasing evaporative water loss in the honey bee *A. mellifera* (Louw and Hadley, 1985), suggesting that carpenter bees may actively promote evaporative water loss at very high T_a s. Tongue lashing at high T_a s has also been reported for *B. vosnesenkii* (Heinrich, 1976) and *C. pallida* (Chappell, 1984). For *A. mellifera*, there exists substantial correlative evidence that active increases in evaporation via the mouth occurs at high T_a s, and that this increase in evaporative heat loss helps bees prevent over-

heating. Restrained *A. mellifera* workers will regurgitate a drop of fluid from the honeycrop onto the labrum and the head surface when heated to T_{th} s of 37–46°C (Esch, 1976; Heinrich, 1980a, b; Louw and Hadley, 1985), which results in an 8-fold rise in evaporative water loss (Louw and Hadley, 1985). This mechanism of thermoregulation appears to be used by *A. mellifera* foraging in the field. The fraction of foragers carrying nectar droplets externally in their mandibles upon returning to the hive increases at high T_a s, with the returning bees carrying droplets between their mandibles having T_{th} s and T_{th} s 1–2°C cooler than bees not extruding droplets (Cooper *et al.*, 1985).

Demonstrating thermoregulation by varying evaporative heat loss requires measurement of the effect of T_a on evaporative water loss. However, only one study to date (Nicolson and Louw, 1982) has measured variation in evaporative heat loss in freely flying bees as a function of T_a . In their study of *X. capitata*, evaporation increased nearly 4-fold between T_a s of 21 and 33°C. This rise in water loss with T_a appears to be passive since water loss during flight was linearly related to vapor pressure deficit (Nicolson and Louw, 1982). The T_{th} s of tethered, flying *X. capitata* at low and high ambient humidities did not differ, suggesting that, for this species, variation in evaporative heat loss isn't necessary for thermoregulation during flight between T_a s of 21 and 33°C.

We have recently measured the effect of T_a on evaporative water loss rates for flying *A. mellifera* (from T_a s of 21 to 44°C) and *C. pallida* (from T_a s of 26 to 36°C). The effects of T_a on evaporative heat loss and metabolic rate were determined for individual *A. mellifera* workers captured as they exited the hive and for individual *C. pallida* males captured as they hovered in defense of territories in the field. Within 1 minute after capture, bees were released them into a 550 ml temperature-controlled glass flight chamber, which was then flushed completely with dry, CO₂-free air and sealed. For those bees that flew continuously for 4–6 minutes, a 50 ml gas sample was withdrawn from the chamber and injected into an air

TABLE 2. Changes in metabolic heat production and evaporative heat loss across air temperature for flying *Centris pallida* males and *Apis mellifera* workers.

Species	T_a range	Δ Metabolic heat production (mWatts g ⁻¹)	Δ Evaporative heat loss (mWatts g ⁻¹)
<i>Centris pallida</i>	26–36	-269	+42
<i>Apis mellifera</i>	21–33	-129	+19
<i>A. mellifera</i>	33–44	-143	+138

stream directed sequentially to an electronic water vapor sensor and a CO₂ analyzer (see closed-system protocols described in Nicolson and Louw, 1982; Louw and Hadley, 1985). Our results suggest that, for both species, variation in evaporative heat loss is a minor component of thermoregulation during flight at moderate T_a s (21 to 36°C). However, for *A. mellifera* at least, evaporation becomes a very important mechanism for preventing overheating during flight at higher T_a s (Table 2).

METABOLIC HEAT PRODUCTION

Variation in metabolic rate and heat production has been reported during preflight warm-up (Heinrich and Kammer, 1973; Heinrich, 1993; Cahill and Lustick, 1976), brood incubation (Heinrich, 1974) and load carriage (Heinrich, 1975; Wolf *et al.*, 1989), but the ability of flying bees to vary metabolic heat production for thermoregulatory purposes has been deemed implausible based on the belief that metabolic rates during flight are determined solely by aerodynamic power requirements (Heinrich, 1993; Heinrich and Esch, 1994). This belief is supported by studies reporting independence of metabolic rate and T_a during free flight (Fig. 3) in *B. vosnesenskii* (Heinrich, 1975), *B. edwardsii* (Heinrich, 1975), *A. mellifera* (Heinrich, 1980b), and *X. capitata* (Nicolson and Louw, 1982). However, using a variety of closed and flow-through respirometry techniques, we have recently found that, for *A. mellifera* workers (Harrison *et al.*, 1996) and *C. pallida* males (Roberts, 1996; Roberts, unpublished data), metabolic rates during flight significantly decrease as T_a rises (Table 2; Fig. 3). For flying *C. pallida* males, the T_{th} excess ($T_{th} - T_a$) decreases by 40% as T_a rises from 26

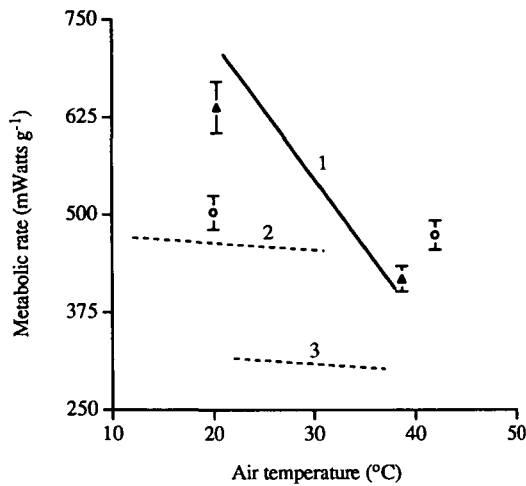


FIG. 3. Metabolic rate vs. air temperature for untethered flying bees. The circles with error bars represent mean (\pm SE) metabolic rates for *Apis mellifera* (means not significantly different: Heinrich, 1980b). The triangles with error bars represent mean (\pm SE) metabolic rates of *A. mellifera* during stationary, undisturbed hovering flight (means significantly different: Harrison *et al.*, 1996). Line 1 is the least square regression of metabolic rate vs. T_a for *A. mellifera* during agitated flight (Harrison *et al.*, 1996). Line 2 is the least square regression of oxygen consumption vs. T_a for *Bombus edwardsii* and *B. vosnesenskii* (Heinrich, 1975). Line 3 is the least square regression of oxygen consumption vs. T_a for *Xylocopa capitata* (Nicolson and Louw, 1982). Solid lines represent significant negative relationships between metabolic rate and T_a , while dashed lines represent non-significant relationships between metabolic rate and T_a .

to 36°C, and is closely matched by the 40% decrease in metabolic heat production across the same T_a range (Roberts, 1996; Roberts, unpublished data). The change in metabolic heat production over this range of T_a s is nearly 6.5 times greater than the change in evaporative heat loss, indicating that variation in metabolic heat production is the primary mechanism of thermoregulation during flight in *C. pallida* males (Table 2).

In our study of flying *A. mellifera* workers, the change in metabolic heat production is over 6 times greater than the change in evaporative heat loss over moderate T_a s (21–33°C), indicating that variation in metabolic rate is the predominant mechanism by which thermal stability is achieved over these T_a s. However, as T_a rises from 33 to 44°C, there is a dramatic rise in evaporative

heat loss which is nearly equal in magnitude to the decrease in metabolic heat production (Table 2), indicating that the two mechanisms are of equal importance to thermoregulation during flight at high T_a s.

The difference between the results of Harrison *et al.* (1996) and those of Heinrich (1980b) regarding the effect of T_a on metabolic rates of flying *A. mellifera* are likely due to technical differences in protocols that produced different intensities of flight behavior. At T_a s near 40°C, the metabolic rates were similar in both studies, but at a T_a of 20°C, the metabolic rates were 30% higher in the study of Harrison *et al.* (1996). The greater intensity of flight behavior (and higher metabolic rates) at 20°C in the Harrison *et al.* (1996) study may have been due to the fact that the bees used in this study were flown for only a few minutes in the respirometry chamber, and always within 5 minutes after capture. In the Heinrich (1980b) study, bees were flown for an average of 9 minutes in the respirometer, 10 minutes after the bees were CO₂ anaesthetized and tarsectomized, and up to 20 minutes after the bees were captured (1980a). If flight and thermoregulatory behavior degrades with time or due to surgery, this may account for the lower metabolic rates in Heinrich's (1980b) study. The difference in results is not due to use of closed-system (Heinrich 1980a) vs. flow-through (Harrison *et al.*, 1996) respirometry, since Roberts (unpublished data) found a similar decrease in metabolic rate with increasing T_a for *A. mellifera* using closed-system respirometry (Table 2). Since the body temperatures of the bees flying in Heinrich's (1980b) respirometer were not reported, it is impossible to determine the extent to which they were thermoregulating. The T_{th} s and T_{abs} s of *A. mellifera* flying in the respirometry chambers used by Harrison *et al.* (1996) closely match those measured for *A. mellifera* flying in a temperature-controlled room (Heinrich 1980a, b) and in the field (Cooper *et al.*, 1985; Coelho, 1991), suggesting that the flight vigor and thermoregulatory efforts of these bees are similar to those of unconstrained flying bees.

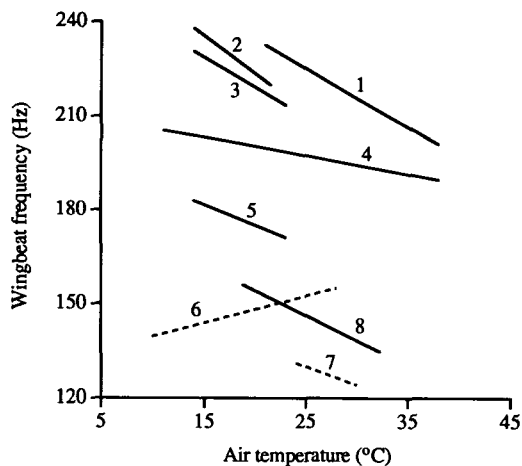


FIG. 4. Least square linear regressions of wingbeat frequency vs. air temperature for untethered flying bees. Solid lines represent significant negative relationships between wingbeat frequency and air temperature; dashed lines represent non-significant relationships. 1 = *Apis mellifera* workers during agitated flight in 300 ml chamber, average mass = 85 mg (Harrison *et al.*, 1996); 2 = *Bombus pratorum* individual foraging in field, average mass of *B. pratorum* = 122 mg (Unwin and Corbet, 1984); 3 = *B. pratorum* individual foraging in field (Unwin and Corbet, 1984); 4 = *A. mellifera* workers entering and exiting hive (Spangler, 1992); 5 = *B. pascuorum* individual foraging in field, average mass of *B. pascuorum* = 131 mg (Unwin and Corbet, 1984); 6 = *Bombus* spp. foraging in the field, average mass = 149 mg (Joos *et al.*, 1991); 7 = *Bombus* spp. hovering in 819 ml chamber, average mass = 175 mg (Joos *et al.*, 1991); 8 = *Centris caesalpiniae* males patrolling at nest emergence site, average mass = 335 mg (Spangler and Buchmann, 1991).

HOW DO FLYING BEES VARY METABOLIC HEAT PRODUCTION?

The ability of a bee to decrease the metabolic cost of seemingly identical flight behaviors as T_a rises suggests an increase in mechanochemical efficiency and/or a decrease in mechanical power output at higher T_a s. Increases in muscle efficiency at higher T_a s could be due to effects of muscle temperature, wingbeat frequency or stroke amplitude on the amount of elastic energy storage, but could also increase due to a greater reliance on an unsteady aerodynamic mechanism (Ellington, 1984; Dudley and Ellington, 1990; Ellington *et al.*, 1996), such as varying the wing's angle of attack, at higher T_a s. Mechanical power output (and metabolic power requirements) during hovering

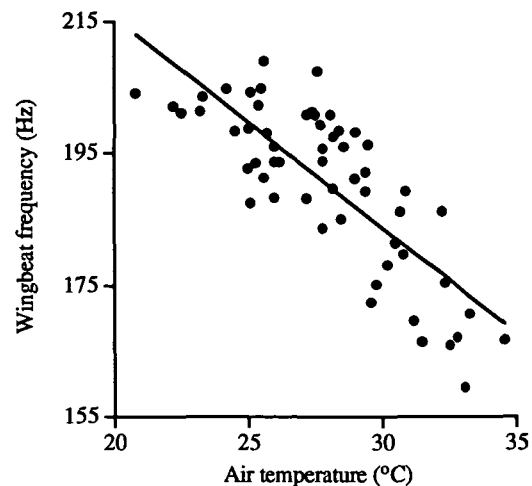


FIG. 5. Effect of air temperature on wingbeat frequency for hovering *Centris pallida* males. The wingbeat frequencies of individual *C. pallida* males were measured with an optical tachometer (Unwin and Ellington, 1979) as they hovered, practically motionless except for the movement of their wings, while defending territories in the field (Alcock *et al.*, 1976; Chappell, 1984). During this territorial behavior, hovering bouts are relatively long, up to 30 seconds, and frequently interrupted by vigorous pursuits of encroaching conspecific males, which last an average of 2–3 seconds (personal observation). Least square linear regression: Wingbeat frequency = $(-3.166 * T_a) + 278.85$, $r^2 = 0.624$, $F_{1,55} = 91.4$, $P < 0.001$. Least square linear regression of wingbeat frequency vs. mass (mg): Wingbeat frequency = $(-0.174 * \text{mass}) + 214.23$, $r^2 = 0.101$, $F_{1,28} = 3.132$, $P = 0.088$. Least squares linear regression of mass vs. air temperature: Mass = $(0.837 * T_a) + 99.25$, $r^2 = 0.014$, $F_{1,28} = 0.407$, $P = 0.529$. Average mass (\pm SE) = $122.1 (\pm 3.7)$ mg, $n = 30$.

flight may be modulated by varying kinematic parameters such as wingbeat frequency and stroke amplitude (Ellington, 1984).

Five out of six studies which have examined the effect of T_a on wingbeat frequency in bees have shown that wingbeat frequency decreases as T_a rises (Figs. 4, 5). In the studies showing a decrease in wingbeat frequency at high T_a s, the variation in wingbeat frequency as a function of T_a is apparently occurring independently of aerodynamic requirements, since the decrease in air density and the increase in kinematic viscosity with rising T_a (Vogel, 1994) predict an increase in aerodynamic power requirements (Ellington, 1984) and, presumably, higher wingbeat frequencies.

Heinrich (1993) suggests that the negative relationship between wingbeat frequency and T_a within foraging *B. pascuorum* and *B. pratorum* individuals (Unwin and Corbet, 1984; Fig. 4) is likely a result of higher nectar and pollen rewards in the cooler mornings than in the warmer afternoons. Since bumblebees rarely fly and allow T_{th} s to fall when foraging from low reward flowers (Heinrich 1972a, b), Heinrich (1993) concludes that the lower wingbeat frequencies reported by Unwin and Corbet (1984) were probably due to cooler T_{th} s in the afternoon. In the only other lab study to examine the effect of T_a on wingbeat frequency in bumblebees, Joos *et al.* (1991) found no effect of T_a on wingbeat frequency among pooled *Bombus* spp. individuals while foraging in the field or hovering in a jar. Thus, the evidence for thermal effects on wingbeat frequency is equivocal for bumblebees. Tentatively, the lack of a T_a effect on wingbeat frequency in bumblebees is consistent with the independence between T_a and metabolic rate for *B. vosnesenskii* and *B. edwardsii* (Heinrich, 1975), although no studies to date have examined the effect of T_a on wingbeat frequency and metabolic rate within a bumblebee species.

In *A. mellifera* workers and *C. pallida* males, which decrease metabolic rates as T_a rises, there is a strong decrease in wingbeat frequency at higher T_a s (Figs. 4, 5) during flight in the lab (Harrison *et al.*, 1996; Roberts, unpublished data) and in the field (Spangler, 1992; Fig. 5). The effect of T_a on wingbeat frequency in *C. pallida* males in the field is not due to size effects on frequency (Casey *et al.*, 1985), as there is no significant correlation between wingbeat frequency and body mass or between body mass and T_a (Fig. 5). The observed decreases in wingbeat frequency and metabolic rate with increasing T_a in *A. mellifera* workers and *C. pallida* males are consistent with the theoretical prediction that mechanical power output (and metabolic rate) should be approximately proportional to wingbeat frequency cubed (Ellington, 1984; Dickinson and Lighton, 1995). However, because power output is determined by many kinematic factors, the extent to which muscle

efficiency or mechanical power output is being varied with T_a is not known. Resolution of this question will require a complete respirometric and kinematic analysis for bees flying across a range of T_a s.

CONCLUSIONS AND FUTURE DIRECTIONS

Despite the fact that it has been known for decades that bees are endothermic and thermoregulate during flight, the mechanisms by which they achieve thermal stability while flying are remarkably poorly understood. Very few studies have simultaneously measured evaporative water loss and metabolic rates in flying bees as a function of T_a , and no studies have directly measured convective heat loss in flying bees. Given the paucity of data, it is difficult to draw broad conclusions, but it tentatively appears that some bees, particularly *Bombus* spp., thermoregulate during flight by varying convective heat loss, mediated by increasing heat flow from the thorax to the abdomen at higher T_a s, while other bees, such as *A. mellifera* and *C. pallida*, lack this ability and achieve thermal stability during flight primarily by varying metabolic rate. Data for a few species, particularly *A. mellifera*, suggest that increasing evaporative heat loss via regurgitation is an important mechanism for preventing overheating during flight at very high ($>35^\circ\text{C}$) T_a s. Considerable comparative research, performed in a phylogenetic context, will be required to determine if there is an adaptive or historical pattern to this variation in thermoregulatory mechanisms.

The finding that some bees can lower the energetic cost of flight at higher T_a s poses very interesting questions about how this apparent increase in locomotory efficiency with T_a occurs. Answering these questions will require examinations of the effects of temperature, frequency and amplitude on insect fibrillar muscle efficiency, and a kinematic analysis of the effect of T_a on flight biomechanics. Another important unanswered question is whether the decrease in metabolic rate is actively controlled by a negative-feedback thermoregulatory mechanism, or whether the decrease in metabolic rate represents an epiphenomenon that occurs secondarily due to an increase in effi-

ciency at higher T_a s. Resolution of this question will be enhanced with further information on T_a effects on muscle efficiency and flight biomechanics, but may also require searching for thermally sensitive neurons and neural control pathways that mediate thermoregulatory responses.

ACKNOWLEDGMENTS

This research was supported by a National Science Foundation Doctoral Dissertation Improvement Grant (IBN-9521543) to S. P. R. and a National Science Foundation Grant (IBN-9317784) to J. F. H. We thank M. A. Weigman for assistance in preparing the line drawing in Figure 1. We thank N. F. Hadley and two anonymous reviewers for helpful comments on the manuscript.

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